

CATERPILLAR LEAF FOLDING AS A DEFENSE AGAINST
PREDATION AND DISLODGMET: STAGED ENCOUNTERS
USING *DICHOMERIS* (GELECHIIDAE) LARVAE ON
GOLDENRODS

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ABSTRACT. Leaf tying and folding are common habits among caterpillars, with a variety of potential functions ranging from alteration of leaf chemistry and microclimate to protection from predators and dislodgment. However, predators may use leaf ties and folds as a cue to caterpillar presence, in which case such refuges could be a liability. I evaluated the protective function of leaf folding in two species of caterpillars (*Dichomeris* spp.) feeding on goldenrods (*Solidago* spp.). Staged encounters confirmed that common field and forest predators (ants and three species of spiders) paid little if any attention to leaf refuges (silk mats of early instar larvae and folds of older larvae), and that they could not penetrate refuges to attack larvae inside. These predators did kill caterpillars outside leaf refuges, although they often overlooked small or less active larvae and had relative difficulty capturing the largest larvae. Leaf refuges also prevented larvae from being dislodged during simulated wind or mammal disturbance to their host plant.

Additional key words: ant, leaf fold, leaf tie, *Solidago*, spider.

Leaf rolls, folds, and ties have long been assumed to protect caterpillars against predators (Frost 1959), and recent experimental evidence confirms that leaf refuges improve caterpillar survivorship specifically in the presence of birds, ants, or wasps (Fowler & MacGarvin 1985, Heads & Lawton 1985, Damman 1987, Atlegrim 1989, 1992, Vasconcelos 1991; but see Ito & Higashi 1991) or more generally where predation and perhaps dislodgment from the host are serious risks (Cappuccino 1993). But leaf refuges can also serve as a cue to predators, and the few detailed observations in the literature suggest that they are not always effective protection. A variety of birds (Robinson & Holmes 1982, Heinrich & Collins 1983, Greenberg 1987) and some wasps (Steiner 1984) open leaf folds to reach the occupants. Other arthropod predators may be attracted to caterpillar leaf refuges as resting sites (Frost 1959, Danthanarayana 1983).

This paper reports observations of some protective functions of leaf refuge-making against predation and dislodgment in the gelechiid caterpillars *Dichomeris leuconotella* (Busck) and *D. bilobella* (Zeller), both of

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which fold leaves on *Solidago* and *Aster* species (Asteraceae) (Hodges 1986, Loeffler 1994). Invertebrate predators are common on these plants. The vast majority of potential *Dichomeris* predators found in surveys of field and forest goldenrods near Ithaca, New York were spiders, followed by ants and occasional reduviids, nabids, cantharids, syrphid larvae, harvestmen, lacewing larvae, asilids, and predaceous mites (Loeffler 1992, 1993; mites may have been more common than observed in these surveys because of their small size, but they are probably relatively ineffective predators of most *Dichomeris* larvae for the same reason). Dislodgment is also a threat to the caterpillars because goldenrod ramets, especially those in forests, are frequently bent or knocked down by falling branches or passing mammals (Loeffler 1992). Caterpillars falling from a host plant often have difficulty locating another, especially where hosts are scattered (Dethier 1959a, 1959b, 1987, Jones 1977, Cain et al. 1985, Damman 1991).

MATERIALS AND METHODS

The caterpillars and their refuges. *Dichomeris leuconotella* and *D. bilobella* larvae differ in their phenology and habitat preferences (Loeffler 1994). In central New York, *D. leuconotella* larvae hatch in late July or early August from eggs laid singly on leaf undersides. First and second instars construct elongate silk webs, up to several times their body lengths. They feed beneath these webs and also exit the refuge at any time of day or night to feed within a few mm of either end (Loeffler 1994). By the third instar, caterpillars are able to pinch or fold the leaf, after which they feed mainly inside the fold. Each caterpillar constructs one to several refuges between hatching and early October, at which time it leaves the plant as a 3-4 mm long third or fourth instar to overwinter in dead leaves on the ground. In late April or May, the caterpillars crawl from the leaf litter onto new goldenrod ramets and begin several weeks of rapid growth accompanied by frequent refuge changes. Sixth (sometimes seventh) instar caterpillars pupate in leaf folds in mid- or late June, and adults fly in late June and early July (Loeffler 1994).

Dichomeris bilobella adults lay eggs in summer, but larvae do not appear on the plants until the following spring. They develop rapidly and conclude their sixth and final instar about two weeks later than larvae of *D. leuconotella*, at a similar size (ca. 16-17 mm). Their leaf folds are much tighter than those of *D. leuconotella*, being barely wide enough to accommodate the larva. *Dichomeris bilobella* is generally more common in forests than in fields, whereas *D. leuconotella* is restricted to open habitats (Loeffler 1994).

Predator trials. I exposed *Dichomeris leuconotella* and *D. bilobella* caterpillars of various sizes to typical oldfield predators (ants) and the

most common forest predators (theridiid, salticid, and araneid spiders) to compare predators' abilities to catch larvae with and without leaf refuges. Voucher specimens of the predators and of *Dichomeris leuconotella* and *D. bilobella* are deposited in the Cornell University Collection under Lot No. 1209. Additional voucher specimens of *Dichomeris leuconotella* and *D. bilobella* are deposited in the U. S. National Museum.

The oldfield predators, *Formica* sp. (of a taxonomically difficult entity within the *Formica fusca* complex, W. L. Brown, Jr., pers. comm.), are large, black, mound-building ants common in many fields near Ithaca, New York. In spring of 1987 and 1988, I allowed 15 fifth instar and 15 sixth (final) instar field-collected caterpillars of each *Dichomeris* species to fold leaves on goldenrod stem tops in vials of water. To assure leaf thicknesses and shapes representative of the variety of *Solidago* species available in nature to *Dichomeris*, I put one third of the larvae in each age group on *Solidago rugosa* Aiton collected from oldfields; one third on *S. rugosa* collected from forest; and one third on the forest species *S. caesia* L. These three types of goldenrod have, respectively: small thick hairy leaves; large, thin, somewhat less hairy leaves; and large, thin, smooth leaves. I ran the final instar *D. leuconotella* trials two weeks ahead of the final instar *D. bilobella* trials, because *D. leuconotella* matures earlier than *D. bilobella*.

After each caterpillar had fully completed its leaf fold atop its respective stem top, I stood the stem top in its vial on a *Formica* mound and allowed ants to crawl over the leaves. I recorded each time that an ant crawled on the leaf with the refuge and larva as an "encounter." After at least six "encounters," I removed the caterpillar from its refuge and returned it to the mound on a second goldenrod stem top, with no refuge. Observations were repeated on this second stem top until six "encounters" had occurred or until the ants had seized the caterpillar or caused it to drop from the stem top. I completed observations on each caterpillar before beginning trials with the next one. In this way, ants were presented with a long alternating sequence of larvae with refuges and larvae without refuges, which should have prevented any effects of order of presentation on ant behavior.

In September, 1987 I repeated this procedure with six third and fourth instar *D. leuconotella* larvae, and I ran additional trials indoors in jars, with 3-6 recently-collected ants per jar, after cold weather made the ants inactive outside. In the indoor trials, where each larva was to be placed with a specific, confined set of ants, effects of order of presentation were of concern. I therefore presented two size-matched larvae simultaneously to each set of ants, with one larva inside a refuge and the other on an unfolded leaf. I presented nine pairs in this way. Additional

tests included introducing larger larvae from a captive colony to test ant response to larval size, and leaving larvae in refuges in the ant jars for a full week.

Exposures to spiders were all made in small jars, by presenting larvae first in leaf refuges, usually for three hours; and then presenting the same larvae on unfolded leaves. This alternating sequence was repeated two to three times for some sets of larvae, to minimize the effects of order of presentation on spider behavior. I collected spiders from goldenrods and asters growing in the forest and placed them individually in the jars 1–2 days before adding a caterpillar. For spring trials I used spiders of a single, extremely common species, the theridiid *Theridion redimitum* (L.). Although these spiders are sedentary webspinners and seemingly unlikely to encounter equally sedentary larvae in leaf folds, I saw *Dichomeris* corpses with such spiders in the forest and concluded that webspinners were a significant threat, especially given their high numbers on the plants (Loeffler 1992). Morris (1972) also documented webspinners preying extensively on caterpillars. For fall trials I used the salticid *Metaphidippus protervus* (Walckenaer) (six individuals used), and the webspinning araneid, *Cyclosa conica* (Pallas) (12 individuals used), which were the two species of spiders most common on forest goldenrods and asters at that time. The lengths of exposures are indicated in Figs. 1 and 2. To factor out effects of a seasonal increase in spider size on capture success of the two species of caterpillars in the spring trials, I used not only field-collected larvae of both species but also *D. leuconotella* larvae from a captive colony that were phenologically synchronized with the later-developing *D. bilobella* and could be tested simultaneously with them. I compared survival rates of these three groups using a G-test with Williams' correction (Sokal & Rohlf 1981).

“Knockdown” trials. To determine whether larvae in refuges are better able to maintain contact with the plant should the plant be knocked to the ground by storms, falling branches, or passing mammals, I again let third to sixth instar larvae of *D. leuconotella* and *D. bilobella* build refuges on stem tops of the three types of goldenrods used for predator trials. Sample sizes for the different age classes of each species ranged from 15 to 38 larvae depending on supply and are indicated in Fig. 3. After refuges were completed, I overturned each stem with its larva onto a piece of paper, letting it fall by the weight of the water vial so that the force of the fall was consistent among stems. I recorded whether larvae maintained their position on the plants or fell onto the paper. Each trial was repeated with the caterpillar sitting outside its refuge, on the upper and then the lower side of the leaf or vice versa, and then once more with the caterpillar inside its refuge.

Time periods: caterpillar in folded leaf
 caterpillar on unfolded leaf

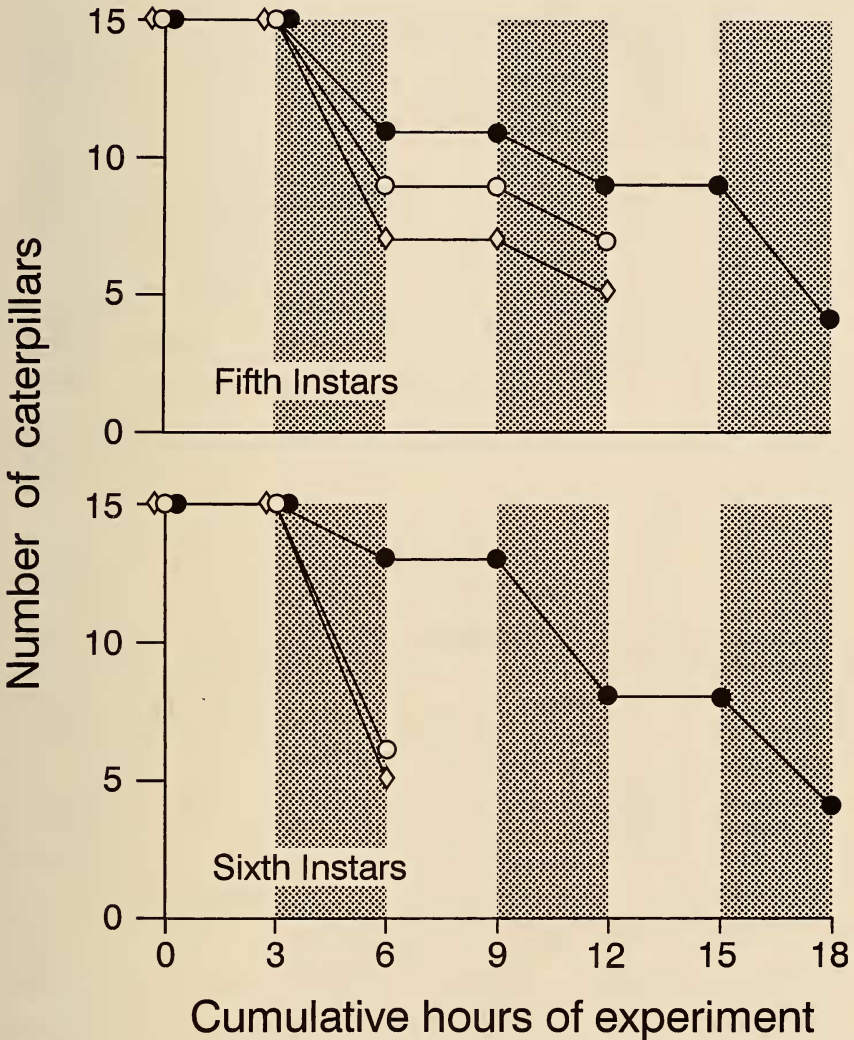


FIG. 1. Results of exposures of *Dichomeris leuconotella* and *D. bilobella* fifth and sixth instar larvae to spiders. Filled circles: field collected *D. leuconotella*, late May to early June 1988. Open circles: captive colony of *D. leuconotella*, early June to early July 1987. Open diamonds: captive colony of *D. bilobella*, early June to early July 1987.

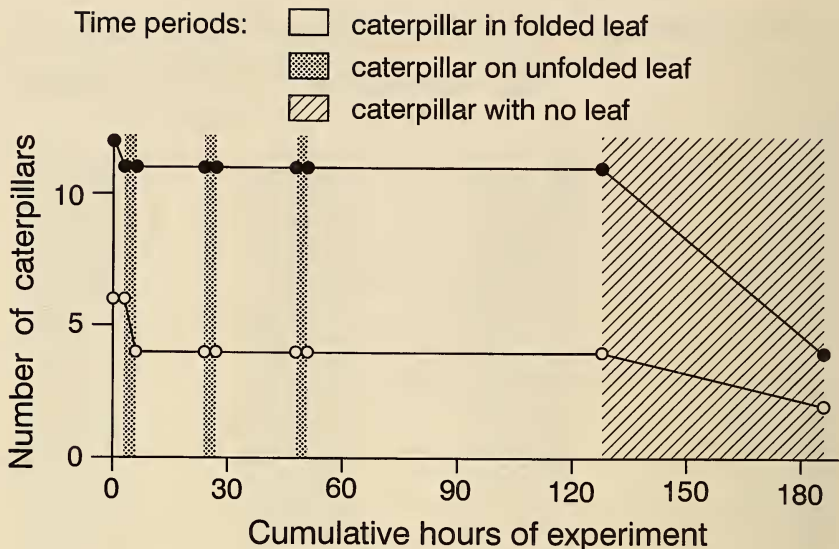


FIG. 2. Results of exposures of *Dichomeris leuconotella* third and fourth instar larvae to spiders in fall, 1987. Filled circles, exposed to araneid; open circles, exposed to salticid.

RESULTS

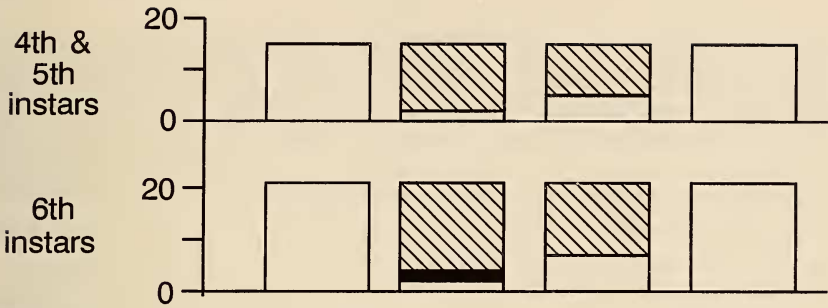
Predator Encounters

Ants and spring-feeding larvae. Results for the three goldenrod types were similar and will be discussed collectively. In general, *D. leuconotella* and *D. bilobella* caterpillars in leaf folds were safe from ant attack. *Formica* individuals crawled freely over the cut stem tops placed on their mounds in late spring. In each of the more than 360 "encounters" between ants and leaves bearing leaf folds with caterpillars, an ant spent from less than one second to more than a minute on the leaf, passing across or along the length of either surface. On 16 occasions, ants bit at the fold, but there was no indication of awareness of the larva inside and on five occasions ants bit more extensively or exclusively on the unrolled portion of the leaf. Such biting might be a means of obtaining water. Ants also bit frequently at other leaves, the stem, and the terminal bud.

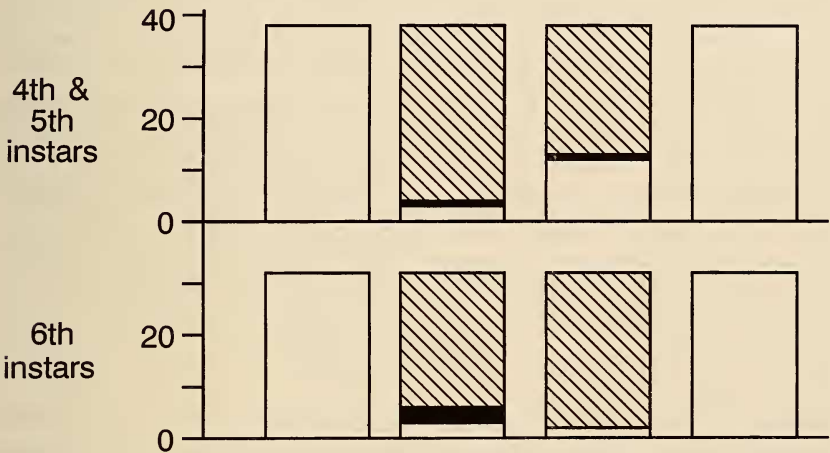
Most of the folds, even those of final instars, appeared to be too narrow for ants to enter. Only three times did ants investigate the entrances of folds, and in the only case in which the ant actually entered the part of the fold occupied by the larva (a final instar *D. bilobella*), it became stuck and struggled for 4 minutes 36 seconds before managing to back out.

Most larvae did not react to ants simply moving over the fold. Reactions of larvae to ants biting or exploring the entrance to the fold in-

Spring: *D. leuconotella*



Spring: *D. bilobella*



Late Summer: *D. leuconotella*

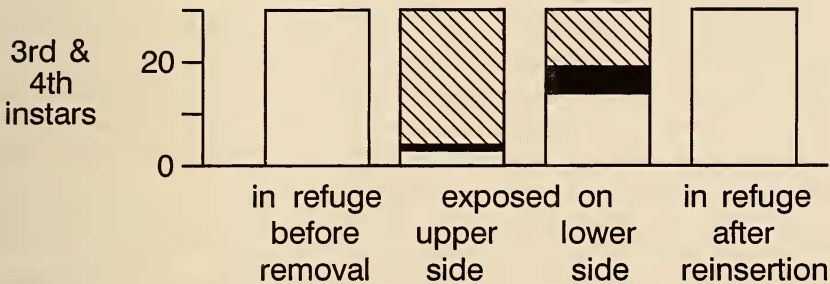


FIG. 3. Results of "knockdown" trials with *Dichomeris leuconotella* and *D. bilobella* fourth to sixth instar larvae in spring, and with *D. leuconotella* third and fourth instar larvae in late summer. Open bars are numbers of larvae that were not dislodged from their position in a refuge or on a leaf when their ramet top was overturned. Hatched bars are number of larvae dislodged from the ramet as it fell; solid bars are number of larvae that were dislodged from the leaf but landed on another portion of the ramet as it fell. The order of four trials was left to right as shown for half of the larvae; for the other half, the third trial (larva exposed on lower leaf surface) was run before the second.

cluded: 1) repeated jerking of the head fore and aft within the fold; 2) partial emergence from the end of the fold opposite the ant, sometimes accompanied by head jabbing and generally followed by quick retreat back into the fold; and 3) in two cases, complete emergence and rapid crawling from the leaf. The only caterpillar captured by ants during such maneuvers was one of the two larvae that emerged completely, the final instar *D. bilobella* in whose fold an ant became stuck. A second ant seized the caterpillar as it emerged from the other end of the fold.

When the surviving 59 larvae were presented on ramet tops without leaf folds (as part of an alternating sequence of larva within fold, same larva outside fold, next larva within fold, etc.), 58 of the larvae were killed or forced to drop from the ramet after a total of 137 encounters. Thus, 79 encounters were "survived on the plant" and 58 involved the caterpillar being killed or losing contact with the plant (Table 1). Caterpillars without folds either sat still or slowly crawled over the leaves and stem of the plant top. Seven larvae began to fold leaves, and occasionally a larva made sufficient progress that I had to reopen the leaf. Ants frequently crawled on leaves bearing larvae without showing reaction to them, even from distances of <10 mm. But at other times ants ran directly to the larvae and attempted to bite them with their mandibles. The larvae reacted with violent wriggling, which, if initiated before an ant had its grip, propelled them to another leaf or off the plant. Sixth instars were more successful at escaping than fifth instars: ants succeeded in capturing 15 of 30 fifth instars on the plants compared to only two of 29 sixth instars (G-test for caterpillar species pooled: $G=14.62$, $df=1$, $p<0.001$; Table 1). An ant biting a caterpillar was usually joined by two or three others that helped subdue the larva and drag it off the plant and down a hole into the mound.

Wriggling was ineffective as a defense on the ground. Of 41 larvae dropping from the ramets (Table 1), ants attacked 22 and killed all of them. This attack rate is of course much higher than caterpillars would encounter in natural vegetation at lower ant densities, and these experiments do not indicate at what rate larvae dropping from a host plant would survive to locate and ascend another.

Only one caterpillar, a sixth instar *D. leuconotella*, remained alive and on the host plant ramet after six encounters with ants. This larva was one of three which sometimes responded to ant approaches by dropping off the leaf and dangling from a silk thread (the other two were fifth instar *D. bilobella*). Such a strategy was successful on four of five occasions, but one *D. bilobella* larva was forced to drop from the thread when the ant plunged after it.

Ants and fall-feeding larvae. Results of exposures of third and fourth instar *D. leuconotella* larvae to ants in September and early Octo-

TABLE 1. Results of exposures of 59 *Dichomeris leuconotella* and *D. bilobella* fifth and sixth instar larvae without leaf folds to ants. An "encounter" is defined as an occurrence of an ant on the same leaf as the larva. Each larva survived 0-6 encounters, for a collective total of 79 (top half of table, total numbers followed by breakdown); the 58 final encounters are indicated in the lower half of the table. In bottom half of table, in all cases, the ant approached within 1 mm.

| | Number of encounters | | | |
|---|------------------------|-----------------|---------------------|-----------------|
| | <i>D. leuconotella</i> | | <i>D. bilobella</i> | |
| | 5th instars | 6th instars | 5th instars | 6th instars |
| <i>Caterpillar survives on plant:</i> | 18 | 21 | 23 | 17 |
| Caterpillar reacts little, ant does not attack | | | | |
| ant on opposite side of leaf | 2 | 6 | 6 | 6 |
| ant on same side, >10 mm from larva | 11 | 9 | 10 | 7 |
| ant within 1-10 mm of larva | 2 | 2 | 1 | 3 |
| ant within 1 mm or contacting larva | 2 | 2 | 3 | 0 |
| Caterpillar drops elsewhere on plant ¹ | 1 | 2 | 3 | 1 |
| <i>Caterpillar killed or drops from plant:</i> | 15 | 14 ² | 15 | 14 ³ |
| Caterpillar drops from plant, | | | | |
| initially unpursued, wanders away | 8 | 14 | 5 | 11 |
| pursued by same ant, captured off plant | 1 | 0 | 1 | 1 |
| Caterpillar siezed by ants on plant | 6 | 0 | 9 | 2 |

¹ After ant approached within 1 mm of caterpillar

² One of 15 caterpillars survived the requisite six encounters on the plant

³ One of 15 caterpillars was killed earlier, when presented to ants inside its leaf fold

ber differed in that both caterpillars and ants showed less response to each other. Refuges of these smaller larvae were either folds or creases bridged by web. Ants several times touched or ran directly over exposed larvae, but in only one case did an ant attempt to bite a larva, and when the caterpillar wriggled out of reach, the ant turned away. Caterpillars generally remained still or edged forward slightly when touched by ants. Only once a caterpillar jumped off the leaf and dangled by a silk thread, hauling itself back onto the leaf after the ant had gone.

However, over a longer time span, exposed larvae were vulnerable. Two larvae that survived six encounters outside refuges were killed subsequently before they had time to construct refuges. In nine trials, I presented size-matched pairs of third and fourth instars to the ants, one in a refuge and the other exposed. The larvae in refuges survived, but seven of the nine exposed larvae were killed, all within approximately 1 h. This difference in survival was highly significant (G-test using Williams' correction, $G=10.59$, $df=1$, $p<0.005$).

Much of the ants' slowness of response appeared to be related to the caterpillars' small size. To test whether the ants would respond to large larvae as they had in spring, I presented one fifth and one sixth instar

D. leuconotella from a captive colony to ants in the field. Both were attacked and killed within five minutes. I also placed one fifth instar and two sixth instar *D. leuconotella* larvae in the same jars in which three third instars had just survived six encounters exposed on leaves. The three large larvae were attacked and killed within 13 min.

In a final series of tests, I left six third or fourth instar larvae in their refuges with the ants, and with additional goldenrod leaves and flowers, for a week. The ants remained healthy feeding on the flowers. All of the larvae survived except one killed toward the end of the week after its leaf turned wholly brown. Leaf senescence often correlates with a larva leaving its refuge (Loeffler, unpubl. data), although I did not determine if in this case the larva left its refuge before it was killed. At the end of the week I removed the remaining five larvae from their refuges and returned them to the jars. Three promptly hid themselves among flowers and two spun normal refuges on leaves. On the following (eighth) day I took the larvae out of their refuges again and removed all flowers from the jars, leaving only leaves. All five larvae were this time killed within 40 min. These results should be interpreted with some caution—they might indicate that ants were more likely to kill when flowers were absent, or that ants were more likely to kill on the eighth day than on the seventh. I consider the former more likely, because the ants fed on the flowers throughout the experiment and killed all five larvae promptly after the flowers were removed. The clear result, however, is that larvae were not killed until after they were taken out of their refuges.

Spiders and spring-feeding larvae. In spring trials, leaf folds of all three goldenrod types protected late instar caterpillars of the two species from attack by individuals of *Theridion redimitum* (Fig. 1). Spiders did not investigate the leaf folds, but sat unmoving in a sparse array of threads as they had in the field when collected. Many larvae emerged partway from their refuges at least once during a three hour exposure, and either fed for several minutes or simply defecated and returned to the refuge. None were caught on these occasions. When I subsequently placed the caterpillars into the same jars without refuges, many of them crawled about extensively. Such movement is not unnatural—after abandoning a refuge in the field, *Dichomeris* larvae often move past several leaf nodes on the stem and explore one to several leaf blades before settling on a fresh leaf and spinning a new fold (Loeffler 1992, 1993, 1994). The spiders often followed the moving larvae and attempted to bite them. The larvae wriggled on contact by the spiders, but some of those which momentarily escaped by this maneuver became tangled in the spiders' sparse webbing. Within an hour, most surviving larvae had ceased wandering and had settled down to fold new refuges. As indicated in Fig. 1, survivors in some groups of larvae were subjected to a

second or even a third round of presentations to the same spiders, first in a refuge for three hours, and then without a refuge. Combining these rounds, the total number of presentations of the 90 larvae first with and then without refuges was 147. The 147 presentations without refuges broke down as follows: on 76 occasions (52%), the larvae survived long enough to initiate a new fold and then survived the remainder of the three-hour test period. On 57 occasions (39%), larvae were killed before initiating a new leaf fold, almost always within an hour of being placed with the spider. On two occasions (1.4%), larvae were killed after initiating leaf refuges. Both cases involved captive colony final instar *D. leuconotella*. Both refuges were still partly open when the spider killed the larva; one was a fold with a 5 mm gap between sides, while the other consisted of a sparsely bound "sandwich" between leaf tips. On 12 occasions (8%), involving both species and both age groups, caterpillars survived a three hour exposure without constructing a refuge. Seven of these larvae and one of the 12 spiders were close to molting, which would account for less active behavior in those individuals.

Field-collected *D. leuconotella* had significantly higher survival rates (80% for age groups pooled in the first three-hour exposure without refuges) than either captive *D. leuconotella* (50%, $G=5.91$, $df=1$, $p<0.025$) or field-collected *D. bilobella* (40%, $G=10.09$, $df=1$, $p<0.005$). These results may reflect the fact that trials with field-collected *D. leuconotella* larvae took place earlier in the season when the spiders were smaller.

Spiders and fall-feeding larvae. Attack rates by the salticid, *Metaphidippus protervus*, and the araneid, *Cyclosa conica*, on third and fourth instar larvae of *D. leuconotella* in late summer were extremely low. The salticids rested on the jar either exposed or under a silk platform, and the araneids perched in sparse cobwebs. The caterpillars likewise moved little, spending their time resting, feeding, or applying silk to the leaves. In a long sequence of alternating exposures with and without refuges, only one larva with a refuge was killed, possibly while out feeding (Fig. 2). This larva was one of 12 exposed to araneids. The remaining larvae survived until the final exposure period, when not only refuges but all leaves were removed from the jars, and seven of the 11 (64%) were killed (Fig. 2). Among the six larvae exposed to salticids, two were killed during the first exposure without refuges, and two more were killed during the final exposure period without leaves. At each of several checks during this final exposure, usually about half of the formerly sedentary larvae were crawling on the jar and the other half were stationary. Both this increased movement and the greater exposure of the caterpillars in the empty jars may have prompted the increased attack rates. Increased hunger of the spiders with the passage of time may

also have contributed to the high attack rate, but had increased hunger been the sole factor involved, one might have expected at least some kills during the lengthy (77 h) period immediately preceding the removal of leaves from the jars (Fig. 2).

"Knockdown" Trials

None of the 106 caterpillars in these trials lost position within a refuge when the ramet tops fell over (Fig. 3). When the caterpillars lacked refuges, the frequency of dislodgment from an upper leaf surface ranged from 81 to 89% in the different age groups and species, while frequency of dislodgment from a lower leaf surface ranged from 53 to 94%. Each of these frequencies differed highly significantly from the zero rate of dislodgment of larvae within refuges ($p < 0.001$ by G-tests for each position of larvae without refuges [upper or lower leaf surface] in each age group of each species). Larvae approaching molts could not maintain a grip on either surface and often fell off even before the sprigs were overturned, thereby demonstrating the necessity of a refuge at such times. Two groups were significantly less often dislodged from the lower leaf surface than from the upper surface: third and fourth instar *D. leuconotella* ($G=13.55$, $df=1$, $p < 0.001$) and fifth instar *D. bilobella* ($G=6.20$, $df=1$, $p < 0.025$).

DISCUSSION

Leaf shelters have a wide variety of potential benefits in addition to protection from predation and dislodgment, such as maintaining a favorable microclimate (Wellington 1950, Henson 1958a, Henson 1958b, Willmer 1980, Hunter & Willmer 1989) and improving the chemical and nutritional suitability of leaf tissue within the shelter (Berenbaum 1978, Sandberg & Berenbaum 1989, Sagers 1992). These functions presumably vary in relative importance among caterpillar species; in some cases, certain effects of leaf shelters may be negative. An obvious example would be the use of leaf folds as a cue by visual predators such as birds which are capable of opening folds.

The ants and spiders tested in this study did not use folds as a cue and could not penetrate them to reach the *Dichomeris* larvae. Folds were effective protection whether they were tight or loose, and whether the leaf was thick or thin, hairy or smooth. The only capture of a larva in a fold resulted from an apparently inadvertent joint effort by two ants. As observed in this study, such instances are probably rare even where ants are concentrated near their nests, or are tending homopterans or lycanid caterpillars.

Smaller spiders, ants, and other predaceous arthropods occur locally that could fit into late instar *Dichomeris* folds, but I have found little ev-

idence during extensive fieldwork that such small predators harm *Dichomeris* larvae.

Predaceous hemipterans may be capable of perceiving the larvae within leaf folds. I have watched a reduviid and a pentatomid waiting beside the entrances to leaf folds; indeed, the reduviid spent two days sitting astride the leaf fold before moving away without capturing the larva. But of predatory wasps and birds, which are potentially able both to associate folds with prey and to enter or open them (Steiner 1984, Damman 1987, Heinrich & Collins 1983), I have neither witnessed nor seen convincing signs of their attack on leaf folds over several field seasons in which I examined many hundreds of folds. Such predators might have much greater impact on tree- or shrub-feeding leaf folders (Heinrich 1979, Holmes et al. 1979).

Danthanarayana (1983) reported that earwigs commonly entered leaf rolls of the light brown apple moth and were important predators of that species. Earwigs were rarely seen on goldenrods in the areas that I worked (Loeffler 1992, 1993, and pers. obs.) and would be unlikely to fit into any but the largest *D. leuconotella* folds.

While leaf folds and webs are generally protective, the sedentariness associated with the leaf-folding habit may also be associated with lower probability of predator attack, inasmuch as it lowers the probability of encounter with sit-and-wait predators such as webspinning spiders. Young leaf folders remain for many days or weeks on a single leaf, and even large *Dichomeris* larvae, which change refuges every few days, move up or down a stem no more than a few nodes when changing refuges. In contrast, exposed feeders on goldenrods move frequently enough that they are rarely encountered near more than a day's worth of feeding damage (pers. obs.). Many exposed feeders, including some on nonwoody plants, are known for their long distance movements, which can average over a meter in a single night (e.g., Hansen et al. 1982). A factor of importance, however, is that many exposed feeders have evolved cryptic styles and timing of movement (Heinrich 1979, Stamp 1984a, Stamp & Bowers 1988, 1992, 1993), whereas *Dichomeris* larvae will move about seemingly indiscriminately at any time of day when feeding or changing refuges (Loeffler 1994, pers. obs.). Thus, although leaf folders are relatively well protected inside their refuges and less disposed to move, when they do move between refuges they may be more vulnerable than larvae of the average exposed-feeding species.

Dichomeris larvae do have two pronounced behaviors that help them escape when outside their folds: wriggling and dropping from the plant, and dropping on a silk thread without losing contact with the host. Both of these escape behaviors are also seen in exposed-feeding species (Allen et al. 1970, Stamp 1984b, 1986). In *Dichomeris* larvae, wriggling

is more effective as an escape mode in final instars than in younger larvae. Reavey (1993) and Stamp (1993) cite other instances in which older instars are less easily killed than younger instars.

Whether or not *Dichomeris* leaf folds also protect against parasitoids was not addressed in the present study, but it seems unlikely. Hawkins and Lawton (1987) found that "semi-concealed" insect herbivores such as leaf folders have relatively large numbers of parasitoid species, and indeed *Dichomeris* larvae have a large parasitoid assemblage (Loeffler 1994) which unlike the predators on goldenrods have apparently evolved mechanisms of dealing with leaf folds and which may indeed use the folds as cues.

The leaf fold also functions to keep *Dichomeris* caterpillars from losing contact with the host plant. The knockdown trials indicated that larvae in leaf folds could maintain their position even during violent movements of the host plant, as during wind storms or passage of a large animal. This function may be particularly important for molting larvae, which do not grip the leaf well. In other experiments (Loeffler 1996), early instars often wandered or fell from plants during refuge changes even though the plants were not disturbed at all. These results of course do not imply that leaf folding is the only or even the best way of maintaining contact with a host plant. Larvae of families such as the Geometridae and Noctuidae that typically feed exposed have a linear arrangement of crochets on their prolegs that enable them to maintain a more solid grip on the plant than can a gelechiid, whose circular arrangement of crochets is adapted for gripping a mat of silk within a refuge (J. G. Franclemont, pers. comm.). Thus, as with predation, dislodgment may be a negligible risk for *Dichomeris* larvae within their refuges but when changing refuges they may be more vulnerable than the average exposed feeder.

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